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The saltatory Origin of Species

BY CHARLES A. WHITE

The following remarks refer to certain noteworthy cases of sudden specific mutation in the genus *Lycopersicum*, and the correlated production of a new horticultural variety of tomato. These remarks will be followed by a comparison of the phenomena referred to with the mutation theory of Professor de Vries and with some of the results of his demonstrative experiments.*

Without reference to the eight or nine other species of tomato that have been more or less satisfactorily recognized by botanists, *Lycopersicum esculentum* has, under American cultivation, become divided not only into a very large number of horticultural varieties, but into at least three distinct groups of those varieties. The varieties, as recognized by gardeners, are mainly, but not wholly, characterized by differences in quality, size and color of the fruit; but the groups are phylogenetic in character and readily recognizable by differences of foliation and inflorescence, and of general habit and relative size of the plants. The color consistence form and size of the fruit, being varietal characters only, are not the exclusive property of any one of these three groups. Two of the groups are known to have originated from the other one; and each one of them embraces a part of the many known varieties. The groups are so distinct from one another, and are characterized by such definite and heritable attributes, that if they had been found in the wild state, no botanist would hesitate to give them new specific names. Their origination under cultivation does not justify one in refusing to apply such names because horticulture does not change the mutative nature of plants. Its nurture and protection give more freedom for normal mutation, as well as for fluctuating and racial variation, than could occur in the wild state. Still, for descriptive purposes in the first part of this article, I will give them the non-systematic name of group, and designate them as the atavic, solanoid and latifoliate groups respectively.

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* See Volume I. of Die Mutationstheorie. Versuche und Beobachtungen ueber die Entstehung von Arten im Pflanzenreich. Von Hugo de Vries. Leipzig, 1901.

The atavic group embraces those decumbent, more or less diffuse, plants with loose foliage, which represent *Lycopersicum esculentum* as it was first horticulturally known, and which now includes the majority of the most approved fruit-varieties. The solanoid group embraces those plants which are often sturdy and more or less upright in posture, and whose compact, rugose foliage has come to be known as the "potato-leaf." It is because the general aspect of the plants often suggests *Solanum* rather than *Lycopersicum* that this group name is given. The solanoid group embraces a considerable number of varieties, but not so many as does the atavic group. A conspicuous feature of the latifoliate group is the character of its leaves, whose petioles are decurrent and whose leaflets are few in number, broad, flattened, and sometimes have their borders entire. The most characteristic member of this group is the variety known to gardeners as the Mikado. It is also sometimes called Turner's Hybrid, but because it is so conspicuously unlike either of its parent forms I think it really originated in correlation with the specific mutation which produced the latifoliate group, and not by hybridization. Other known members of this group are yet very few. The members of each of these three groups are more or less true to their own seed as regards the characteristics of both group and variety, but the cases of sudden mutation which I am about to describe constitute a special deviation from that rule as do also the cases of original mutation, which produced in correlation with that act, the first varieties of the solanoid and latifoliate groups.

My observations were made while engaged in amateur gardening upon my house-lot in Washington, D. C., and were briefly as follows: In the spring of 1898 I purchased from a dealer in Washington two dozen tomato plants of the Acme variety and transplanted them in my small garden. They produced a uniform crop, both fruit and plants answering in all respects to the reputed characteristics of the Acme, the plants of which variety are typical representatives of the atavic group. I selected seeds from fruit of the best plants of the crop and planted them in the same garden plot in 1899, expecting to grow another crop of Acme tomatoes from them. The seeds germinated promptly and the crop of thirty young plants grew well, but from their first appearance above ground they showed a marked difference from Acme plants. When they had reached the fruiting stage they had developed into typical representatives of the solanoid group, and not of their parent atavic group ; showing that the difference from their parent form was more than varietal in character. Furthermore, every plant of that crop possessed identically the same characteristics, all having shared equally and fully in the mutation. The new form was varietally characterized by an excellent quality of fruit, but it was different in flavor and shade of color from that of the Acme, and ripened earlier than did that of the parent plants. I saved no seed from the fruit of the new variety and therefore supposed it to be lost, as indeed it was.

In 1900 I planted in the same garden-plot Acme tomato seed which I purchased from a seedsman who grew it on a Pennsylvania farm, more than a hundred miles from the place where the seed of my first crop was grown. These seeds also produced a uniform crop of typical Acme plants and fruit. I selected seeds from fruit of the best of that crop of thirty Acme plants and sowed them in my garden in the spring of 1901, and grew in that year also thirty plants from those seeds, again expecting to get a harvest of Acme tomatoes. On the contrary, the result was an exact duplication of my experience of 1899, every plant and every fruit partaking fully and uniformly in the duplicated mutation. *

One naturally inquires whether mutation of any other variety than the Acme would have occurred in my garden, whether it is an inherent quality of that variety to give only one mutative result, and that toward the Solanoid group, and what are the natural and artificial conditions of my garden. I have made no experiments with any other varieties than the Acme and its progeny, the new one, and can therefore only refer to these. The Acme variety is now about twenty-five years old, and has been one of

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* An account of these two mutations of identical character was published in Science for November 29, 1901, but a sufficiently clear distinction between the combined varietal and specific characteristics of the plants resulting from that mutation was not therein made. That statement also was written from a horticultural rather than from a botanical standpoint.

the most stable of the many known varieties of tomato; but of late years it has shown so much tendency to atavic reversion that gardeners are abandoning its cultivation. Possibly that senile decline of varietal characters with which the true specific attributes were long blended, has left the latter with more freedom for mutation. Still, it cannot be supposed that such a condition is the rule for all mutating plants, and it will presently be shown that mutation sometimes occurs in the first generation of a species following its own origin by mutation.

Two dozen plants of the new variety from seed of the second mutation observed by me are now, July 15, 1902, growing vigorously in my garden and bearing characteristic fruit. Every plant is true to seed in both varietal and specific characteristics and the new variety, which I have called the Washington, gives promise of being heritably stable. It shows no tendency to either varietal or specific change, although growing under the same conditions which attend both the mutations which I have described and with which it originated.

There is nothing unusual in the physical conditions and environment of my garden. The soil is clayey, formerly part of a cultivated field, fertilized with stable manure and sodium nitrate, and watered with Potomac water. The seeds were germinated in window boxes, in garden soil, and transplanted on different ground for each year, soon after the spring frosts ceased. I do not know that any other case of mutation has ever occurred in the district which is occupied by the same soil and subject to the same environing conditions.

The new fruit compares favorably with the most approved varieties, and is therefore horticulturally valuable. But that fact is of little importance compared with the biological questions which arise concerning the mutative origin of the plant which bore it. I shall, therefore, in this article make no further reference to the fruit and discuss only the biological significance of the plant-mutation of which it was the joint product. The new variety, however, will be of botanical interest as a demonstration of the heritable character of varieties originating in correlation with specific mutation.

The sudden origination of new plant-forms having hitherto been believed by many persons to be always due to hybridization, I refer to the following facts as proof that there was no cross-fertilization in either of the two cases mentioned, and that the new form is therefore not a hybrid. In neither of the two cases mentioned was any other variety of tomatoes grown with those which I planted, and no other grew in my neighborhood. Wind, or insect cross-fertilization was therefore quite improbable. Because I personally gathered, preserved and planted all my seed and cultivated all my plants, I am sure no substitution of either seed or plants occurred. The fact that in both those cases of mutation every plant of the whole crop partook equally of that act is itself proof that cross-fertilization did not occur. If my Acme plants had received adventitious pollination, or if pollen had reached them from any other flowers than those of their connate crop associates, the results of that cross-fertilization would necessarily have been incomplete as to the whole crop. It would also have been various as to the kinds of hybrids produced had the pollen come from more than one variety. Even if it were credible that the first case of complete mutation of the whole crop might have been the result of cross-fertilization from some unknown source, it would still be too much to believe that exactly the same result could have been produced a second time in successive years by such adventitious means. Therefore the question of hybridity is eliminated.

The origination of this new form was, in both instances, saltatory. It occurred in correlation with the ordinary function of intraspecific reproduction and was therefore accordant with both physiological and phylogenetic law. It did not result from cross-fertilization, and it is therefore assumed to have been a spontaneous result of some not yet ascertained exciting cause, and primarily due to some unknown determinate or predisposing cause.

After I had reached the foregoing conclusion as to the nature of the mutations which I had witnessed, public announcement was made of the publication of Professor de Vries' theory of mutation already referred to, and I at once began a comparison of his theory and observations with my observations which are described in the foregoing paragraphs. This comparison convinced me that my cases of mutation are similar in fundamental character to those described by Professor de Vries, and the brief discussion I shall give them will be in accordance with that conviction. But to illustrate my remarks upon them it is necessary to briefly state the nature of his mutation theory and the methods he has pursued in demonstrating it; and also to show wherein it differs from the generally accepted Darwinian theory. For the sake of brevity these statements are mostly made in epigrammatic form. It is my purpose also, as far as possible, to present this brief sketch of the theory and its demonstration from the author's point of view, albeit in words of my personal choosing.*

The Darwinian theory of the origin of species by natural selection teaches that species have been produced from one another, through lines of genetic descent, by a process of evolutional variation which is immeasurably slow, even in its most accelerated cases; that one of the chief causes of specific change is the competitive struggle for existence to which all organisms are subjected; and that variation is incipient species-building. The enunciation of this theory was a strong and effective plea in favor of the origin of species by the operation of natural law as opposed to the then-prevailing belief that every organic form has arisen by a special act of creation. It has served a grand purpose, especially in establishing the doctrine of evolution on a firm basis, and if its candid and eminent author were now living he would be among the first to welcome any change in it that might prove to be necessary in view of later discovered facts.

The de Vriesian theory of mutation is in entire accord with natural law and also with the doctrine of the evolutional origin of species through lines of genetic descent, but it especially makes a clear distinction between species and varieties and teaches the sudden origination of the former whether they possess more or less strongly marked attributes. It also teaches a far more stable entity of species than one can conceive of who unqualifiedly accepts the Darwinian theory. Professor de Vries logically assumes that the mutation theory is as applicable to animals as to plants, but he has formulated it only with reference to the latter. I shall make only a similar reference to the theory in following paragraphs, although my former paleontological work suggests a much wider application of it.

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* A somewhat fuller, but brief, statement of the mutation theory is given by me in the Annual Report of the Smithsonian Institution for 1901. An interesting general sketch of the theory by Professor de Vries is contained in Science for May 9, 1902.

The theory begins with a philosophical concept concerning the molecular constitution of the protoplasm of organisms, as set forth in the author's treatise on intracellular pangenesis.* It assumes that the specific attributes of multicellular plants result from the special molecular constitution of their protoplasts, or cell contents; and that these attributes are built up of sharply defined intracellular units, which normally combine in groups. This specific group-combination has much stability, but it is subject to change by sudden, independent action of some unknown determinate cause. That change is the initial step in mutation and consists of the addition, or substitution, of one or more units to an established group and the consequent rearrangement of the units of that group, forming a new one.

Upon the integrity of the groups of units depends the stability of the specific attributes. Their normal tendency to stability is so great that initial group-changes do not occur in the somatoplasts of plants but only in the plasma of certain of their reproductive cells; and they occur there only seldom. Ordinarily, when such a change occurs, it is only in the oöplast of the germ cell of the ovule which is about to originate a new plant. If no change of specific units occurs in the oöplast the case is one of ordinary reproduction. If such a change does occur in the oöplast the case is one of mutation as well as of reproduction, all the cells of the coming plant naturally partaking of the same specific attributes.

It should be here remarked that such cases as the reputed origination of the nectarine from the peach are apparent exceptions to the rule just mentioned. That case being one of ordinary asexual reproduction and if it really was also a case of simultaneous origination of a new species, initial mutative change must have occurred in the plasma of the apical cell of the mutating bud. If mutation may occur in correlation with asexual reproduction, mutative molecular change in pollen cells would seem to be unnecessary in mutating cases of sexual reproduction.

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* See Intracellulare Pangenesis. Von Hugo de Vries. Pp. 212, Jena, 1889.

Mutation is, therefore, the saltatory origination of new organic species resulting from sudden molecular change in their initial protoplasts. The new species is at once such, without preliminary preparation, without intermediary gradation, and without any subsequent addition of attributes. Newly mutated species differ clearly and distinctly, but not widely, from the parent species. Wide differences between species of a genus indicate the death of intervening species. As a rule, mutation occurs, not by, or in connection with cross-fertilization, but in correlation with pure intraspecific sexual reproduction, and nevertheless independently of it. A new and stable specific form is thus produced, but the parent species remains intact. Mutation is, therefore, a strictly phylogenetic process, although plural cases occurring in one and the same mutating species are often randomly divergent in character.

Hybridization occurs in nature, and very often in cultivation, but it is not mutation. Neither is it really phylogenetic in character, but a result of ontogenal miscegenesis, with the groups of molecular specific units unbroken in each parent germinal portion. According to Mendel's law, even fertile hybrids are sooner or later obliterated by the prepotency of one or the other of the parent forms.

Mutation, being a normal process, does not produce monstrosities. The latter are cases of distorted or abnormal ontogeny.

Above all, variation is not mutation, nor are varieties incipient species. Ordinary fluctuating, or individual, variation is an inseparable accompaniment of all plants, and racial variation also widely prevails, but no kind of variation leads to mutation proper.

Mutation, being a result of intracellular molecular change, is necessarily sudden, as is molecular substitution in chemical reaction. One cannot concieve that molecular change could continue in action toward one result through immeasurable time. A species being suddenly produced implies that its normal state is one of at least a considerable degree of stability.

Species being normally stable and only incidentally mutable, a part of the time-existence of each is therefore a mutative, and a part an immutative, period. The immutative period is, as a rule, so very much longer than the mutative period that very few mutable plants exist simultaneously in any flora. Because of these facts, of the great prevalence of fluctuating varieties, and for other reasons, mutation has hitherto usually escaped observation, even by naturalists.

When a new species originates by mutation in the wild state it is at once subject to the usual competitive struggle for existence, even with its parent form. Species not only do not originate by natural selection and the struggle for existence, but they perish thereby; and the number of species which have originated by mutation since the beginning and met an untimely death without having produced any progeny, is doubtless beyond human estimate.

Acting upon the theory which is very briefly stated in the foregoing paragraphs, Professor de Vries formed a systematic plan for discovering and studying mutating plants. He selected from the flora of Holland more than one hundred species and transplanted them in experimental gardens at Amsterdam, where he also sowed seed of those, and many other members of the Holland flora. He also made exhaustive studies of that flora in its wild state. The object of these experiments was not to produce horticultural varieties but to discover plants that were already in their natural mutative period among the multitude that were plainly immutative. He nurtured, protected and artificially pollinated the plants thus growing under his care. In short, he fully supplied their natural wants, gave them much greater advantages of growth and development than the best wild conditions could afford, and relieved them from all the adverse conditions which they necessarily would have encountered in their wild habitat. Meanwhile he eagerly watched them all for any sign of mutation that might occur.

The result was at least one grand success amid a multitude of failures. The failures were not due to the method of investigation, but to the fact that almost all the plants investigated were in their immutative period. The chief case of success was with plants of the American genus *Oenothera*, the so-called evening primroses. One species, *O. Lamarckiana*, proved to be in an exceptionally mutable condition. A few years ago it escaped from cultivation in certain parks in Holland and immediately began a most vigorous multiplication and dispersion in a wild state. Among the abundant original plants thus produced, two new species soon appeared which Professor de Vries believed had originated then and there by mutation from *O. Lamarckiana.* He transferred many of those plants and much of their seed to his experimental gardens and there verified that belief by obtaining a repetition of those two mutations under his direct observation. Furthermore, in the course of a few years of experimentation, he obtained by mutation from *O. Lamarckiana* five other new species, seven in all. A part of these new species proved to be also mutative, adding still other new ones to his list; and all the new ones possessed, from the moment of their origin, well-defined and heritable attributes. These mutations occurred in the progeny of plants which had received intraspecific artificial pollination. Interspecific pollination, or cross-fertilization, was not found to facilitate mutation, and hybridization was not sought for or desired.

In view of the success of Professor de Vries' experiments with *Oenothera*, and the fact that all except one or two per cent. of the species with which he experimented failed to show any sign of mutation; and the further fact that he experimented with only a part of the Holland flora, one infers that the proportion of immutative plants to the mutative may perhaps be as great throughout the plant kingdom as he found it to be in that flora.

Recognizing the fundamental accordance of my observations with those of Professor de Vries, I assume that *Lycopersicum* is, like *Oenothera*, in its mutative period and that *L. esculentum* has given mutative origin to two other species which, in previous paragraphs, I provisionally designated as groups. The fact that these two specific forms differ less from each other, and from their common parent *L. esculentum*, than do some other species from one another, does not affect the validity of the claim that they should also be regarded as distinct species. The facility with which all forms of *Lycopersicum* hybridize with one another also does not affect that claim because of the non-phylogenetic character of hybridization. I shall therefore apply the systematic name of *Lycopersicum solanopsis* to the solanoid group, and the latifoliate group accordingly becomes *L. latifoliatum;* but the atavic group must retain its original name of *L. esculentum.*

While the cases of mutation which I have observed in *L. esculentum*, fundamentally accord with those which Professor de

Vries observed in *Oenothera Lamarckiana*, they present some peculiar features, the chief of which are shown by the following comparisons. In none of his cases do specific attributes seem to have been complicated with varietal characters, unless one should except the case of *O. nanella*. Perhaps a sufficient reason therefor is that most of the species of *Oenothera* have hitherto shown very little tendency toward variation. On the contrary, *Lycopersicum solanopsis* became divided into several varieties soon after its first mutation from *L. esculentum*. I do not know in what variety it first appeared, but in the first of the two subsequent mutations, those which. I observed, it appeared in a new variety, the Washington. Furthermore, in the next mutation, which was quite independent of the others, it appeared in the same variety. Indeed, in all the cases of specific mutation of *Lycopersicum* to which I have referred, some one horticultural variety seems to have been a conjunctive vehicle for the introduction of the new species.

The scope of mutative action in *Oenothera* has been given in detail by Professor de Vries, but my observations show that in *Lycopersicum* the scope of that action is different in certain respects. He found mutation in *Oenothera* to act independently and separately upon the germ of each one of a very small number of seeds in an abundant fruitage of a large crop of plants; and that those seeds were usually subject, not to one and the same mutation, but to different specific mutations. I found in *Lycopersicum* that one specific mutation acted completely and uniformly upon the germs of all the seeds, of all the fruits, of every plant of my crop of 1899, and that it acted in precisely the same manner in the crop of 1901. The suddenness of its action in the latter crop especially, is shown by the fact that the Pennsylvania Acme seeds, planted in my garden in 1900, gave a full and uniform crop of true Acme plants; and that it was their seed which mutated so completely upon the same ground in 1901. In view of my repeated experience with the Acme variety one seems to be justified in assuming that the determinate cause of mutation is now latent in every plant of that variety wherever grown, and that it quickly manifests itself when the flowering plants are brought under the influence of a favorable, exciting cause.

Again, Professor de Vries found that some of his newly mutated species of *Oenothera* were themselves immediately mutable. My observations of the mutation from *Lycopersicum esculentum* to *L. solanopsis* seem to indicate that the mutative act was coincident with impending varietal senility in the Acme variety, and that the resulting variety, the Washington, has no tendency to mutate. Doubtless *L. esculentum* originated by mutation from some other pecific form of that genus, but no evidence seems to be obtainables that, although variable, it began to be really mutable until many years after the species became horticulturally known. These facts indicate that in some species the mutative period occurs in one part of their time-existence, and that in other species it occurs in another part of the same.

Some of the observations made by myself in the cases of mutation of *Lycopersicum* are thus seen to be different from any of those made by Professor de Vries in cases of mutation of *Oenothera;* but the facts which we have both observed are not in conflict. Their differences only indicate that the field of investigation which that distinguished botanist has opened in close contact with nature is a very broad one.

SMITHSONIAN INSTITUTION, 15 July, 1902.